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the hairs and glands may also save the plant from destruction by animals.

Of one thing the writer is certain, that these delicate objects are interesting to study. Situated as they are in immense numbers and in such great variety on the surface of so many plants, they are easily obtained and easily prepared for examination. They are excellent objects for a beginner in the use of the compound microscope; and for protracted and careful experiments, they are worthy the skill of the most accomplished scientist. In them we may spend weeks to advantage in observing the development of cells, the nucleus and nucleoli, and the gyration of the sap. In form and color they are exquisitely beautiful, while in variety they are inexhaustible.

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ON THE TRANSFORMATIONS AND HABITS OF THE BLISTER-BEETLES.

BY CHAS. V. RILEY, A.M., PH.D.

[*Continued from the April Number.*]

History of Epicauta.—It is generally stated by writers on the Hive-bee that the Oil-beetle (*Meloë*) is one of its parasites. The possibility that our more common blister-beetles were similarly parasitic on bees, taken in connection with the frequent complaints from apiarians of the wholesale death of bees from causes little understood, led me, some years since, to pay attention to the biological characteristics of the blister-beetles, in the hope of ascertaining whether or not they really bear any connection with bee mortality. From these investigations I am satisfied that *Meloë* is only parasitic on the perfect Hive-bee as it is on so many other winged insects that frequent flowers; and that it cannot well, in the nature of the case, breed in the cells of any social bee whose young are fed by nurses in open cells.

I have had no difficulty in getting the eggs or the first larva of several of our vesicants, and described some of them at the Hartford (1874) meeting of the Am. Ass. Adv. Sc.; but these young larvæ refused to climb on to plants furnished to them, or to fasten to bees or other hairy insects. Nor would they nourish upon honey, bee-bread, or bee larvæ on which they were placed. They showed a proclivity for burrowing in the ground, and acted quite differently from those of *Meloë* or *Sitaris*, which not

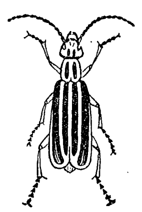

FIG. 3—*Epicauta vittata:* normal form.

only readily attach to bees in confinement, but which, in the case of *Meloë*, I have known to so crowd upon mature hive bees as to worry them to death and cause extended loss in the apiary. Explorations into the nests of Solitary bees gave no clue, and, in fact, the immense numbers in which the more common blister-beetles occur, rendered a parasitic life upon such bees highly improbable. In sweeping plants and flowers with the net, I had never met with any of the first larvæ with which I had become familiar, as already indicated; while I had on several occasions, in digging ground where there was no trace of bee nests, met with the curious pseudo-pupa so characteristic of the family. While analogy and the law of unity of habit in species of the same family pointed, therefore, to a parasitic life, I began to conclude, from the facts just stated, that the parasitism was of another kind, having satisfied myself by various experiments that the triungulins did *not* feed on roots. Few discoveries are stumbled upon. We find as a rule that only which we anticipate or look for. In 1876, in digging up the eggs of the Rocky Mountain locust (*Caloptenus spretus*) at Manhattan, Kansas, the pseudo-pupæ were not unfrequently met with. The thought at once occurred to me that locust eggs might be the proper food for these blister-beetle larvæ, and it was encouraged by the fact that the Meloids abound most in those dry western regions where the Acrididæ most prevail, and by a pretty distinct recollection, which my notes support, that the years when the vesicants were most injurious to potatoes had been preceded by dry Falls, during which there had been much locust injury and, necessarily, unusual locust increase. The suspicion thus raised that these blister-beetles preyed in the preparatory states upon locust eggs was confirmed last spring by finding the larvæ of different ages within the egg-pods and devouring the eggs of *Caloptenus spretus*. Mr. A.N.Godfrey had, also,

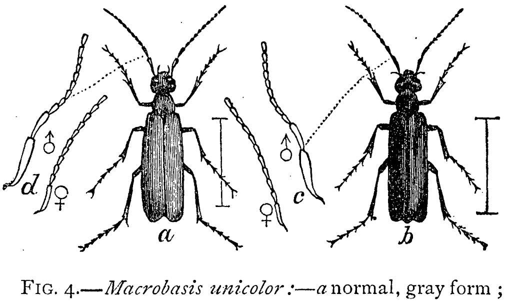

FIG. 4.—*Macrobasis unicolor:*—*a* normal, gray form; *b*, black (*murina*) form; *c*, *d*, male and female antennæ of either.

no difficulty, under my directions, in finding them last May at Manhattan; while they were sent to me among other locust-egg parasites by Mr. Seth H. Kenney of Morristown, Minn., and from St. Peters in the same State by Prof. Cyrus Thomas.

From such larvæ preying on the eggs of *C. spretus* I have reared the unicolorous form of *Epicauta cinerea* (Forster), or the margined Blister-beetle[1]; the *Epicauta pensylvanica* (DeGeer),[2] or the Black Blister-beetle; the *Macrobasis unicolor* (Kirby)[3] or the ash-gray blister-beetle; and the form of it described as *murina* by LeConte, or the black-rat blister-beetle.

Since then I have found it very easy to trace the larval habits and development of the two more common potato-feeding species around St. Louis, viz: the striped blister-beetle (*Epicauta vittata*, Fabr.)[4] and the Margined Blister-beetle (*marginata* Fabr.) just alluded to.

Careful examination of locust eggs in the vicinity of potato fields frequented by these beetles show a varying proportion of the egg-pods affected, and in some locations nearly every pod of the differential locust (*Caloptenus differentialis*) will contain the *Epicauta* larva. The eggs of this locust are laid in large masses of 70 to about 100. The pod is but slightly bent, rather compact outside, while the eggs are irregularly ar-

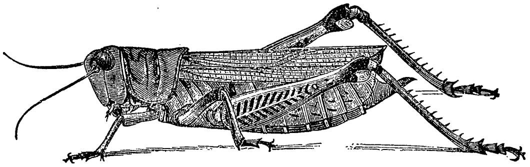

FIG. 5.—*Caloptenus differentialis.*

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[1] The black, gray-margined form, very appropriately described by Fabricius as *marginata*, is referred to *cinerea* Forster by modern systematists, and specifically united with it by Dr. Horn. Yet the fact remains that the two are not ordinarily, if ever, found commingled. The margined form is very common in potato fields in Missouri. It shows little variation and is found almost invariably in conjunction with *vittata*, but not with the unicolorous form in question, which is most common farther west and occurs abundantly without the margined form—all which is against the specific union of the two.

[2] = *E. atrata* Fabr.

[3] = *M. cinerea* Fabr., *Fabricii* Lec., *murina* Lec., *debilis* Lec. I accept Dr. Horn's conclusion that the last two are but poorly developed forms of this species. Yet the *murina* form is not due to rubbing or injury, but issues from the pupa without a trace of gray scales on the elytra.

[4] = *E. lemniscata* Fabr. Dr. Horn retains *lemniscata* as a distinct species in his Revision already referred to. The outer stripe in the bi-vittate specimens divides up in others so as to give the tri-vittate character on which *lemniscata* is founded. Both extremes and every possible variation between them occur constantly together in the same potato field in Missouri, and there are no other differences of specific value.

ranged, and capped with but a shallow covering of mucous matter. It is the egg-pod of this species which the larvæ of the two Blister-beetles in question prefer; for while they will feed upon those of other species in confinement, I have so far found none in the deeper-necked, narrower, more compact egg-pods either of *Caloptenus femur-rubrum*, *C. Atlantis*, or *Œdipoda sulphurea*, in which the eggs are regularly and quadrilinearly arranged, as in those of *C. spretus*. Not only have I found a large proportion of the egg-pods of *C. differentialis* naturally infested with these *Epicauta* larvæ, but I have succeeded in hatching and rearing numbers in-doors.

From July till the middle of October the eggs are being laid in the ground in loose, irregular masses of about 130 on an average —the female excavating a hole for the purpose, and afterwards covering up the mass by scratching with her feet. In confinement she sometimes omits both these instinctive acts and oviposits on the surface of the ground. She lays at several different intervals, producing in the aggregate probably from four to five hundred ova, judging from examinations made on the ovaries of some that were gravid. She prefers for purposes of oviposition the very same warm sunny locations chosen by the locusts, and doubtless instinctively places her eggs near those of these last, as I have on several occasions found them in close proximity. In the course of about 10 days—more or less, according to the temperature of the ground—the first larva or triungulin hatches. The hatching takes place without the aid of any *ruptor ovi*, for the egg-shell is so delicate that it easily splits, from mere expansion, along the back near the head, and breaks and shrivels up with the escape of the larva. These little triungulins (Pl. 1., Fig. 2), at first feeble and perfectly white, soon assume their natural light brown color and commence to move about. At night or during cold or wet weather all those of a batch huddle together with little motion, but when warmed by the sun they become very active, running with their long legs over the ground, and prying with their large heads and strong jaws into every crease and crevice in the soil, into which, in due time, they burrow and hide. Under the microscope they are seen to fairly bristle with spinous hairs, which aid in burrowing. As becomes a carnivorous creature, whose prey must be industriously sought, they display great power of endurance, and will survive for a fortnight without food in a moderate temperature. Yet in the search for locust eggs many are, without doubt, doomed to perish, and only the more fortunate succeed in finding appropriate diet. Upon the slightest disturbance they curl up in a ball with the head bent pretty closely on the breast.

Reaching a locust egg-pod, our triungulin, by chance, or instinct, or both combined, commences to burrow through the mucous neck, or covering, and makes its first repast thereon. If it has been long in the search, and its jaws are well hardened, it makes quick work through this porous and cellular matter, and at once gnaws away at an egg, first devouring a portion of the shell, and then, in the course of two or three days, sucking up the contents. Should two or more triungulins enter the same egg-pod, a deadly conflict sooner or later ensues until one alone remains the victorious possessor. By the time the contents of an egg are consumed, the body of the parasite has perceptibly increased so that the white sutures between the segmental plates show conspicuously, especially as there is a tendency on the part of the animal to curve its body, and bring the sutures more into relief. A second egg is attacked and more or less completely exhausted of its contents, when a period of rest ensues, the triungulin skin splits along the back and there issues the *Second Larva* (Pl. I., Fig. 4)—white, soft, with reduced legs and quite different in general appearance from the first. This molt is experienced about the eighth day from the first taking of nourishment. The animal now naturally lies in a curved position (Pl. I., Fig. 4, *d*), but, if extracted from the egg-pod, will stretch itself and move with great activity, reminding one very strongly of many Carabid larvæ, for which reason I would designate this as the *Carabidoid* stage of the second larva. After feeding for about another week, a second molt takes place, the skin, as before, splitting along the back and the new larva hunching out of it until the extremities are brought together and released almost simultaneously. This kind of molting, which is characteristic of our blister-beetles up to the pseudo-pupal state, is exceptional among insects, the skin being ordinarily worked backward from the head. The modification at this molt is slight. The mouth-parts and legs become rudimentary and the body takes on more fully the clumsy aspect of the typical Lamellicorn larva, for which reason I designate this as the *Scarabæidoid* stage of the second larva.

Another six or seven days elapse and the scarabæidoid skin is rent and shed with but slight modification in the form and characters of the animal. In this, the Ultimate stage of the second larva (Pl. I., Fig. 5) the creature grows apace, its head being constantly bathed in the rich juices of the locust eggs, which it now rapidly sucks or more or less completely devours. The color is more yellowish than it was before, and the power to stretch and travel on the venter on an even surface is still retained. In another week it forsakes the remnants of the pabular mass, and, by burrowing a short distance in the clear soil, avoids the deleterious decaying influences of these egg remnants. In the soil it forms a smooth cavity, within which it lies stretched on one side, motionless and gradually contracting. The skin separates and becomes loose at the end of the third or fourth day, when it splits on the top of the head and thoracic joints and is worked toward the extremity, but never fully shed. The mouth-parts and legs are now quite rudimentary and tuberculous, the soft skin rapidly becomes rigid and of a deeper yellow color, and we have what has been called the semi-pupa (Pl. I., Fig. 8). The term pseudo-pupa given it by Fabre is more appropriate, and I should prefer myself to call it the *coarctate larva*, for it is nothing but a rigid and dormant larval stage, having its counterpart in the well-known "flax-seed" stage of the Hessian-fly larva and in the so-called coarctate pupa of the Diptera generally. A similar dormant but less rigid larval stage occurs with many Tenthredinidæ in Hymenoptera, and, in fact, the summer dormancy of certain Lepidopterous larvæ and the winter dormancy of others is analogous. We find something similar, therefore, in all the orders undergoing complete transformations, but in no insects is the change so marked and exceptional or the freeing of the subsequent larva from the coarctate larva so striking as in these Meloidæ. The insect has the power of remaining in this coarctate larval condition for a long period, and generally thus hybernates.

In spring the coarctate larval skin is, in its turn, rent on the top of the head and thorax, and there crawls out of it the *Third Larva*,[1] which differs in no respect from the ultimate stage of the second larva already mentioned, except in the somewhat reduced size and greater whiteness. The coarctate skin, when deserted, retains its original form almost intact. The third larva is rather active, and burrows about in the ground; but while there seems to be no reason why it should not feed, nourishment is not at all essential, and all my specimens have, in the course of a few days, transformed to the true pupa without feeding. In the transformation to pupa (Pl. I., Fig. 9) the third larval skin is worked into a wrinkled mass behind, as is also the skin of the true pupa when shed. The pupa state lasts but five or six days, and before the wings of the imago are fully expanded, or the abdomen contracted, the general aspect of *Epicauta* forcibly recalls the mature *Henous*.

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[1] The coarctate larva is, properly speaking, the third, and that following it the fourth; but just as I have preferred to designate as special stages of the second larva the stages between the first and fourth molts, so I prefer to call the last larva the third, to conform to the nomenclature now generally employed.

Like all parasitic[1] insects that nourish on a limited amount of food and possess no power to secure more, the blister-beetles vary greatly in individual size in the same species, and the larvæ have the power of accommodating their life to circumstances, and of assuming the coarctate larval form earlier or later according to the size of the egg-mass which they infest. I have had some interesting illustrations of this in my experiments with them. In an average sized egg-pod of the differential locust, however, there are more than enough eggs to nourish the largest specimen of *E. vittata*, and a few are usually left untouched.

The period of growth, from the first feeding to the coarctate larva, averages, as will be gathered from the foregoing, about a month; yet in the month of September, out-doors, under screens where I have had the differential locust oviposit for the experiment, I have known the full larval growth of *E. vittata* to occupy but 24 days. As this species occurs in the beetle state as early as June in the latitude of St. Louis and as late as October, there are possibly two annual generations here and farther south.

Larval Habits of Macrobasis and Henous.—The characteristics of the triungulins of the blister-beetles, represented by *Epicauta* and *Henous*, are remarkably similar, and point to unity of habit. The same holds true of the characters of the second, coarctate and third larva and of the pupa of *Epicauta* and *Macrobasis*. They are precisely alike; so that, while appreciable differences may be found in the triungulins, it is doubtful whether the subsequent developmental stages will indicate specific or even generic differences in species of similar size in these three genera.

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[1] An insect is not properly parasitic that simply feeds on eggs, but the term is permissible and even necessary to characterize and distinguish those species which develop within and are confined to a locust egg-pod, from the predaceous species that are not confined but pass from one pod to another.

That the eggs of *Epicauta* may exceptionally hybernate is possible, but, from their delicate nature, improbable. That the triungulins frequently do so there can be no doubt, especially in species like the Black Blister-beetle, which is found on the flowers of Solidago, Eupatorium, etc., till the end of October, and continues laying till frost. I have at the present time (November) many of these last that are quietly huddled together, and, with winter temperature, will doubtless remain so; while others have worked in between the locust eggs, there evidently to remain without feeding till spring opens. I have also found as many as five triungulins of this species curled up in the deep red mucous matter that surrounds the eggs of *Œdipoda phanœcoptera*—all numb and torpid, and evidently hybernating.

Conclusion.—From the foregoing history of our commoner blister-beetles, it is clear that while they pass through the curious hypermetamorphoses so characteristic of the family, and have many other features in common, yet *Epicauta* and *Macrobasis* differ in many important respects from *Meloë* and *Sitaris*, the only genera hitherto fully known biologically. To resume what is known of the larval habits of the family, we have:

1st—The small, smooth, unarmed, tapering triungulin of the prolific *Sitaris*, with the thoracic joints subequal, with strong articulating, tarsal claws on the stout-thighed but spineless[1] legs, and, in addition, a caudal spinning apparatus. The mandibles scarcely extend beyond the labrum; the creature seeks the light, and is admirably adapted to adhering to bees but not to burrowing in the ground. The second larva is mellivorous, and the transformations from the coarctate larval stage all take place within the unrent larval skin.—We have:

2d—The more spinous and larger triungulin of the still more prolific *Meloë*, with long caudal setæ, but otherwise closely resembling that of *Sitaris* in the femoral, tarsal and trophial characters, in the subequal thoracic joints, in the unarmed tibiæ, and in the instinctive love of light and fondness for fastening to bees. The second larva is also mellivorous, but the later transformations take place in the rent and partly shed skins of the second and coarctate larvæ.—We have:

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[1] The larva of *S. humeralis* appears to differ from that of *S. colletis* in having hairs on the femora and tibiæ.

3d.—The larger and much more spinous triungulins of the less prolific *Epicauta*, *Macrobasis*, and *Henous;* with unequal thoracic joints, powerful mandibles and maxillæ, shortened labrum, slender femora, well-armed tibiæ, slender, spine-like, less perfect tarsal claws—combined with an instinctive love of darkness and tendency to burrow and hide in the ground. The second larva takes the same food as the first, its skin is almost entirely cast from the coarctate larva, while the subsequent changes are independent and entirely free of the shell of this last.

Larval Habits of Cantharis.—The question naturally arises here, whether *Cantharis*, in its larval habits, will most agree with *Meloë* and *Sitaris* or with *Epicauta.* The triungulin, except in becoming almost black, has much in common with *Meloë*, in the subequal thoracic joints, and the long antennæ; also in its habit, observed by Lichtenstein, of fastening to bees.[1] The fact that it can nourish on honey, though it does not appear to do so freely, would also indicate that it breeds in the nests of solitary bees. Nevertheless, in the slender thighs and the caudal and abdominal characters it agrees more nearly with *Epicauta*, and in the stage following the first molt the legs are still quite long and the general aspect much like the carabidoid stage of that genus. I should not be surprised, therefore, if *Cantharis* also nourished on locust eggs.

What is Known of the Larval Habits of other Meloid Genera.—*Mylabris* Fabr. (*nec* Geoff.), according to V.-Mayet, is much less prolific than any Meloids so far observed. The egg is 2.5 mm. long and is ½ as wide, with a tolerably thick shell and the embryo more fully bent within it. The triungulin has many of the characters of *Epicauta*, judging from the published description (*Ann. Soc. Ent. de Fr.*, 1876, p. cxcvi.), which is, however, not sufficiently detailed as to the trophi. I doubt not that the genus will be found to infest locust eggs.

Horia Fabr., from what little is known of it, would seem to have a similar partial parasitism to *Meloë*, but on carpenter bees.

Tetraonyx Latr., was found by Guérin-Meneville in places frequented by bumble-bees.

The eggs of *Apalus* Fabr., as well as its triungulin, are said to resemble those of *Meloë.*

Zonitis Fabr., is known to develop in the cells of *Osmia* and *Anthidium*, and to have a coarctate larva much like that of *Sitaris.*

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[1] Since this was published M. Lichtenstein writes me: "They only fasten to bees when enclosed in tubes with them. At liberty they do not climb flowers, like *Meloë*, in search of bees, but run quickly on the soil, just as you describe for *Epicauta*."